

Abstract—We verified the age and growth of swordfish (*Xiphias gladius*) by comparing ages determined from annuli in fin ray sections with daily growth increments in otoliths. Growth of swordfish of exploitable sizes is described on the basis of annuli present in cross sections of the second ray of the first anal fins of 1292 specimens (60–260 cm eye-to-fork length, EFL) caught in the region of the Hawaii-based pelagic longline fishery. The position of the initial fin ray annulus of swordfish was verified for the first time with the use of scanning electron micrographs of presumed daily growth increments present in the otoliths of juveniles. Fish growth through age 7 was validated by marginal increment analysis. Faster growth of females was confirmed, and the standard von Bertalanffy growth model was identified as the most parsimonious for describing growth in length for fish greater than 60 cm EFL. The observed growth of three fish, a year-old in size when first caught and then recaptured from 364 to 1490 days later, is consistent with modeled growth for fish of this size range. Our novel approach to verifying age and growth should increase confidence in conducting an age-structured stock assessment for swordfish in the North Pacific Ocean.

Age and growth of swordfish (*Xiphias gladius*) caught by the Hawaii-based pelagic longline fishery

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Swordfish (*Xiphias gladius*) constitute an economically important fishery resource and have historically supported many large-scale commercial fisheries throughout the world's oceans. During the 1990s, however, declining catches and average sizes of swordfish in Atlantic and Mediterranean fisheries indicated possible or likely overexploitation of these populations, and the status and management of these stocks became a highly publicized issue.

Swordfish began to be a major species targeted by the Hawaii-based pelagic longline fishery in 1990 and continued as such through the late 1990s, with landings peaking at 4000–6000 t in 1991–93 (Ito et al., 1998). This longline fishery targeted swordfish within, and adjacent to, fronts of the Subtropical Convergence Zone north of Hawaii during winter and late spring (Bigelow et al., 1999). Beginning in 1999, gear restrictions were imposed and in mid-2001 a moratorium on shallow-set (swordfish style) longlining within the swordfish fishery grounds north of the equator was instated to reduce interactions of fishing gear with, and incidental take of, protected species—primarily loggerhead turtles (*Caretta caretta*). The moratorium was lifted in March 2004 and a regulated (by annual effort cap, gear restrictions, take limit) longline fishery was reinstated.

A preliminary stock assessment for swordfish caught in the North Pacific Ocean, based on surplus production models, was conducted in early 1999 and was updated in early 2002 to include body length composition. No age-structured assessment as yet exists for swordfish in the central North Pacific. With the subsequent re-opening of the Hawaii-based fishery, there has been renewed interest in swordfish management in the North Pacific and a recognized need for a more robust, age-structured basis for stock assessment and documentation of age distributions and growth rates. For example, Sun et al. (2005) recently assessed the population status of swordfish taken by the tuna longline fishery in the waters around Taiwan in the western North Pacific.

Our objectives in this study were the following: 1) to evaluate the accuracy and precision of our age estimates; 2) to provide several complementary data supporting a predictable periodicity (on a yearly basis) of annulus formation in cross sections of anal-fin rays of swordfish caught in the region of the Hawaii-based longline fishery and examine evidence verifying our age estimates for these specimens; and 3) to estimate sex-specific patterns of size-at-age and growth to provide input for pending age-structured assessments of swordfish stock(s) in the central North Pacific.

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Materials and methods

Collections and measurements of fish

All swordfish used for age determination in this study were collected from within the general region of the Hawaii-based pelagic longline fishery (Ito et al., 1998; DeMartini et al., 2000, Fig. 2 therein). About 95% of the specimens used were caught by commercial longlines during March 1994–June 1997; specimen collections were conducted and fish measurements were recorded by National Oceanic and Atmospheric Administration (NOAA) Fisheries, Southwest Region observers. The remaining 5% of the fish were caught on research cruises conducted during April–May 1992 and 1993, September 1996, and March–April 1997. Fish were measured (eye-to-fork length, EFL, in cm) before dressing (removal of head, entrails, tail, and fins) at sea. As they were dressed, sex was scored according to macroscopic criteria and later validated by microscopic evaluation of histological preparations of gonads for subsamples of the fish (DeMartini et al., 2000). When the fins of swordfish were removed at sea, either a portion or the entire first anal fin was collected and frozen. The braincase section, including the region of the semicircular canals was collected from juvenile and young adult swordfish, either when fish were beheaded at sea or when whole frozen bycatch specimens were thawed and dissected ashore. Additional larval and early young-of-year specimens (4 mm to 20 cm EFL) were collected by a neuston trawl (5-mm and 0.505-mm mesh in wings and codend, respectively) leeward of Hawaii Island during 1995–97; intact specimens were stored frozen before otolith extraction.

Laboratory processing and specimen examination

Frozen first anal fins were thawed, and the second spiny ray was selected (Berkeley and Houde, 1983), removed, and cleaned of all tissue. It was then dried in a dehydrator for 24–48 h at about 60°C, and three adjacent, transverse sections were cut with a low-speed saw. The first cut was made according to standard protocol (Ehrhardt et al., 1996) but at a newly defined position (distal end of the medial suture, hereafter “suture terminus”) located about 15% of the distance beyond the basal condyle. Subsequent cuts were made distal to the first, spaced to provide wafers ≈1 mm thick (Uchiyama et al., 1998). The location chosen for the cuts was different from the conventional standard (i.e., at a distance above the basal condyle equal to one-half the condyle width= $d/2$) currently used in swordfish aging studies (Sun et al., 2002). The unconventional cut was necessary because the condyle of the second ray is often severed or lost during the removal of fins by fishermen at sea. A small series of matched (same fish) fin ray samples were cut at the suture terminus and at the $d/2$ positions; some of these were also cut immediately distal to the condyle (basal cut) and the numbers of annuli were counted and compared. Cross sections of rays were preserved in mounting media on glass microscope slides and stored

(without cover slips) in sealed boxes. Otoliths (sagittae) were dissected from frozen larvae and young adults at the NOAA Fisheries, Pacific Islands Fisheries Science Center (Honolulu Laboratory), and stored dry after having been cleaned, rinsed with water, and dried with 95% ethanol (EtOH).

Fin ray annuli, each defined as a single pair of opaque and translucent bands completely encircling the cross-section hemisphere without partial and split checks (Ehrhardt et al., 1996; Sun et al., 2002), were enumerated. At first examination, about 1% of all cross sections were deemed unreadable and discarded. The distances separating the distal edges of the translucent band of each annulus were measured, the opaque versus translucent nature of cross-section edges was noted, and marginal increment ratios (MIRs) were measured in marginal increment analysis (Campana, 2001). A series of MIRs was calculated for each specimen of age 1 or older by using the formula (Prince et al., 1988; Sun et al., 2002):

$$MIR = (R_{tot} - R_n) / (R_n - R_{n-1}),$$

where R_{tot} = total radius of fin ray specimen; and R_n and R_{n-1} = the distance from ray focus to the n th and $(n-1)$ th annuli, respectively.

The focus was identified at the proximal confluence of growth striations (Ehrhardt et al., 1996). Because only one image analyzer was available and multiple readers had to work concurrently, several methods were used to examine specimens: 1) slide-mounted ray cross sections were viewed with a dissecting microscope (10–60×) by reflected light against a black background; 2) grey-scale TIFF file images of slide-mounted cross sections were prepared by using a digital camera system (Sony DKC-5000 and VCL-713BXS macro-zoom lens; Sony USA, New York, NY), processed to enhance contrast and sharpness using Adobe PhotoShop vers. 3, and viewed by means of two shareware available in the public domain (NIH Image vers. 1.58; National Institutes of Health, Bethesda, MD; and Scion Image vers. Beta 4.0.2; Scion Corporation, Frederick, MD), for MAC and PC, respectively. Annuli were counted independently by two primary readers (1 and 2) without reference to length, sex, or month of capture. Each reader made two or more readings, spaced by at least several months to cloak the identity of individual specimens. Presumed daily growth increments (DGIs) were enumerated by using digitized composite images (scanning electron micrographs of sagittae) (Humphreys, 2000).

If known-age specimens are unavailable for use in calibrating age assignments, a reference collection should be evaluated and a consensus or majority agreement used to provide a reference standard (Campana, 2001). We therefore enlisted the services of four other North and South Pacific laboratories that either recently had or were presently conducting aging studies of swordfish (Institute of Oceanography, National Taiwan University [NTU]; the National Research Institute of Far Seas

Fisheries [NRIFSF], Japan; the Centro de Investigacion Cientifica y de Educacion Superior de Ensenada [CICESE], Mexico; and the Instituto de Fomento Pesquero [IFOP], Chile). They provided 20 representative and usable fin ray specimens for swordfish caught by their respective regional fisheries. Specimens spanned all available months of capture and body sizes of both sexes.

Specimens were processed in identical fashion within each laboratory (e.g., the $d/2$ cut was used by the Honolulu Laboratory for select Hawaii-based fishery specimens). Digitized images of all 100 specimens were prepared at the Honolulu Laboratory and file images were distributed among laboratories. Most laboratories conducted multiple readings by two or more readers, thus enabling evaluation of precision and bias within and among laboratories.

Statistical analyses

Conventional descriptive statistics (Zar, 1984) were used to evaluate several interrelated data necessary for verification or corroboration of annular periodicity and size-at-age. We evaluated interrelations among fin ray radius (in mm) and estimated age (in days) based on enumeration of DGIs and EFL (in cm). Regression models were fitted by using nonlinear least squares (Marquardt algorithm) and the best model was chosen on the basis of relative r^2 values (proc nlin, SAS, vers. 8, SAS Inst., Inc., Cary, NC). Likely sexual dimorphisms in relationships (Sun et al., 2002) were evaluated with ANCOVA (proc glm; SAS, vers. 8, SAS Inst., Inc., Cary, NC).

Standard graphical methods and statistics (Campana, 2001) were used to evaluate between- and within-reader bias (age-bias plots) and precision gauged by the coefficient of variation (CV: deviation [=SD] (100/mean) (Campana et al., 1995; Campana, 2001). Observer bias (accuracy) also was evaluated partly in terms of the majority agreement standard generated by the aforementioned inter-laboratory calibration exercise. Precision was evaluated by comparing the repeatability of estimates made by readers 1 and 2 for both the specimen series provided by the inter-laboratory exercise and the much larger group of specimens that were used for the main study described in this article. CVs were compared both within- and between-readers.

Growth was described by fitting fin ray-based age estimates to back-calculated body length-at-age by using von Bertalanffy growth formulas (VBGFs). Both standard and generalized VBGFs (Richards, 1959) were evaluated:

$$\begin{aligned} \text{Standard VBGF: } L_t &= L_\infty (1 - e^{-k(t-t_0)}); \\ \text{Generalized VBGF: } L_t &= L_\infty (1 - e^{-K(1-m)(t-t_0)^{(1/(1-m))}}); \end{aligned}$$

where L_t = mean eye-to-fork length (EFL, in cm) at age t ;

L_∞ = asymptotic length;

t = a specific age;

t_0 = hypothetical age at length zero;

k and K = growth coefficients; and
 m = fitted fourth parameter.

Individual length-at-age was back-calculated by using method II of Sun et al. (2002) which is based on the formula of Ehrhardt et al. (1996):

$$EFL_t = (R_n/R_{tot})^b EFL,$$

where EFL_t = back-calculated eye-to-fork length at age t ;

R_n and R_{tot} are as previously defined; and

b = parameter derived from the relation of EFL to R_{tot} .

EFL was related to R_{tot} using the power equation,

$$EFL = a R_{tot}^b,$$

where a , b = fitted parameters.

This model was chosen because of the obvious curvilinearity of the relationship. Sex effects were evaluated by using ANCOVA.

Likelihood ratio (LR) tests (Cerrato, 1990; Quinn and Deriso, 1999) were used to evaluate the effects of sex and type of VBGF model for describing the length-at-age relationship. For LR test statistics, the additivity of untransformed data was assumed and the statistics were calculated as two times the log-likelihood:

$$LR = [-n/2] [\ln(2\pi[SSE/n]) + 1],$$

where SSE = error sum of squares; and
 n = number of age classes.

In both cases, LR test statistics were compared against χ^2 with $df = 1$ by using the Akaike information criterion.

Results

Accuracy and precision

A pilot evaluation of the two methods used for viewing fin ray preparations (microscope, digital image analyzer) indicated nearly congruent results (mean difference only 0.12 ± 0.087 yr or 3% of a mean age of 3.8 years; matched-pairs t -test; $t=1.38$; $P=0.17$). Directly viewed and image analyzed preparations were therefore considered equivalent (no bias from methods) and were pooled in all subsequent analyses.

Age-bias plots for readers 1 and 2 indicated variable deviations, small in relation to the age estimates, which lacked major pattern over the range of all putative ages. Reader 1's mean age estimates regressed on reader 2's age estimates deviated insignificantly from a slope of 1 and an intercept of 0, even if additional positive deviations for ages > 8 were included (Table 1A). Readers

Table 1

Summary statistics from a comparison of the (A) bias (accuracy), and (B) precision (repeatability) of swordfish (*Xiphias gladius*) ages estimated by readers 1 and 2; precision was evaluated both between- and within-readers. Bias and precision were evaluated by age-bias plots and coefficient of variation (CV), respectively (Campana et al., 1995; Campana, 2001). Sexes were pooled in (A) because the effect of sex insignificantly influenced aging differences between readers, both for ages <8 and for all ages (ANCOVA: $P=0.21$ and 0.06 , respectively). H_0 = null hypothesis. SE = standard error.

A Hypothesis	Main study data subset	Parameter estimate \pm SE (test statistic)	df	Prob > F
Bias				
H_0 : slope = 1	ages < 8	0.985 \pm 0.034	1,6	0.67
H_0 : intercept = 0		($F=0.20$) 0.015 \pm 0.078 ($F=0.04$)	1,6	0.85
H_0 : slope = 1	all ages	1.010 \pm 0.019	1,10	0.93
H_0 : intercept = 0		($F=0.01$) -0.006 \pm 0.070 ($F=0.27$)	1,10	0.62
B				
Type	Specimen series	Median CV ¹	Number of fish	
Precision				
Within-reader, reader 2	inter-laboratory ²	9.7	100	
Within-reader, reader 1	main study	13.3	377	
Within-reader, reader 2	main study	12.9	790	
Between-reader	inter-laboratory	15.7	100	
Between-reader	main study	10.8	1055	

¹ Weighted equally over all age groups.

² Unavailable for reader 1, who made only one set of readings.

1 and 2 aged specimens used in the inter-laboratory calibration exercise with negligible (<2%) deviation from the majority agreement standard. The age assignments of both readers 1 and 2 were henceforth used for growth analyses. If the readers did not agree, reader 2 re-examined the specimen to resolve the discrepancy. Specimens with unresolvable ages were omitted from subsequent analysis.

Age estimates were adequately precise, as well as accurate. CVs of within- and between-reader age estimates were generally 10–15 % (Table 1B). CVs of the inter-laboratory and main study readings were similar, as were the within- and between-reader CVs within each series (Kruskal-Wallis 1-way ANOVAs; all $P>0.3$).

Verification and validation of annuli

The results of marginal increment analysis (Fig. 1) provided consistent quantitative support for the contention that fin rays form a single pair of opaque and translucent bands per year (Campana, 2001). Formation of the annulus is complete by September in central North Pacific swordfish; MIRs were wider in June and narrower in September (for fish of both sexes) than during the rest of the year (2-way ANOVA on

sex and month; interaction effect: $F=0.80$, $df=11,732$, $P=0.64$; month effect: $F=2.05$, $df=11,743$, $P=0.02$). The pattern generally applied to fish of all ages through at least age-group 7 of adequate sample sizes (Fig. 1), although considerable variability existed throughout the year.

Verification and corroboration of annuli (Kalish et al., 1995; Campana, 2001) were further explored using several complementary methods. These consisted of comparisons of ages that were based on otolith sagittae and fin rays from matched (same) fish and on quantitative relations among fin ray cross-section dimensions, fish body length, and ages based on sagittal DGIs and fin ray annuli. Measurements of total and incremental radii in fin ray cross-sections were obtained for a total 1336 swordfish (733 females, range 46–260 cm EFL; 603 males, range 36–229 cm EFL). Numbers of DGIs on sagittae were enumerated for a total 63 larval, older juvenile, and small adult swordfish of the two sexes (range 4–135 cm EFL). The EFL-at-age relation was described for 49 fish (range 4–133 cm EFL) for which there were adequately precise DGI counts. Fin ray preparations were available for 50 specimens with matched DGI counts.

Total cross-section radius of the second ray of the first anal fin was significantly related to fish age in days for

older juveniles and small adults (Fig. 2). The best fitted power equation relationship:

$$R_{\text{tot}} = 0.0197 \text{ DGI}^{0.7877}, r^2 = 0.877,$$

predicted an R_{tot} of 2.055 ± 0.069 (mean \pm SE) mm at an age of 365 days. For a larger sample of fish aged to be 1 yr old by using fin rays, the radius R_1 (the just-completed first annulus) was 2.23 ± 0.091 mm from the focus on cross sections cut as described and was unrelated to sex of fish (Student's $t=0.88$; $n=71$ fish; $P=0.38$).

Cross sections taken at the suture terminus were located about 14% of the conforming total length (distal surface) of the ray above the condyle. In a comparison between cross sections from matched (same) fish, where the cross sections were taken at our suture terminus and the $d/2$ position for 115 specimens (sexes pooled) ranging from 82–241 cm EFL, the conventional cross-section radius was located at a shorter average distance (about 10%) above the condyle. Total radii of cross sections produced by the two different types of cuts nec-

essarily differed slightly (by 3%; ANCOVA; $P<0.001$) but were independent of fish size and sex (ANCOVA; $P=0.6$ and 0.3 , respectively). Despite these numeric differences, there was no discernible average difference in annuli counts with sections cut at the suture terminus and $d/2$ positions. Core regions of basal cut sections were obscure in 77% of the specimens whose ages ranged from 1 to 11 years (ages estimated by using suture terminus sections). Either the first annulus was missing or the section could not be aged for 21% of the basal cut specimens. Ages averaged 0.8 yr younger with basal sections (matched-pairs signed-ranks test; $P<0.01$) for 25 of the specimens whose age estimates differed between basal and distal sections, and averaged 0.2 yr younger overall. For basal cuts only, mean back-calculated body lengths at age 1 yr, based on the presumed "first annulus," differed in predicted fashion among age groups (i.e., they were greater for older fish in which the real first annulus was more apt to be missing with age (2-way ANOVA on age-group and type of section; age-group effect: $P<0.0001$; Penha et al., 2004).

Daily growth of young swordfish based on counts of DGIs on otoliths corroborated our estimates of size-at-age for age-group 0 (age 0+) and yearling fish based on fin ray cross sections (Fig. 3). Body length was nonlinearly related to presumed age in days and the most parsimonious, best fit was the hyperbolic, two-parameter relation:

$$\text{EFL} = (136.6 \text{ DGI}) / (140.8 + \text{DGI}), r^2=0.937, n=49.$$

This best fit relation indicated a body length of 98.6 ± 3.0 (95 % CI) cm EFL at an age of 365 days (Fig. 3).

Development of growth model

The relations between EFL and cross-section fin ray radius were strongly curvilinear, and doubly log-transformed data differed in elevation for females and males (ANCOVA; $F_{1,1333}=6.41$; $P=0.01$) but shared a common slope (ANCOVA; $F_{1,1332}=0.84$; $P=0.36$). For R_{tot} measured in mm and EFL (in cm), the best fit relations were

$$\begin{aligned} \text{Females } \text{EFL} &= 64.3725 R_{\text{tot}}^{0.5539}, r^2=0.939; \\ \text{Males } \text{EFL} &= 66.3090 R_{\text{tot}}^{0.5175}, r^2=0.936. \end{aligned}$$

R_{tot} regressed on EFL indicated that R_1 should be about 2.16 mm, using the independent length-at-age 1-yr estimate of 98.6 cm EFL. An R_1 of 2.055 mm would be equivalent to a length of about 96 cm EFL (Figs. 2 and 3).

Table 2 lists our sex-specific, back-calculated EFL-at-age estimates. Summary statistics for the corresponding estimates of ray radii are provided in Table 3 for males and females, respectively, by age group and averaged over all age groups. We estimated an age of 0.58 yr (213 days) at an observed mean EFL of 82.2 cm from the otolith-based length-at-age relation (Fig. 3) and used this estimate to represent the mean length of age-group-0 fish ≥ 60 cm EFL in the aged population.

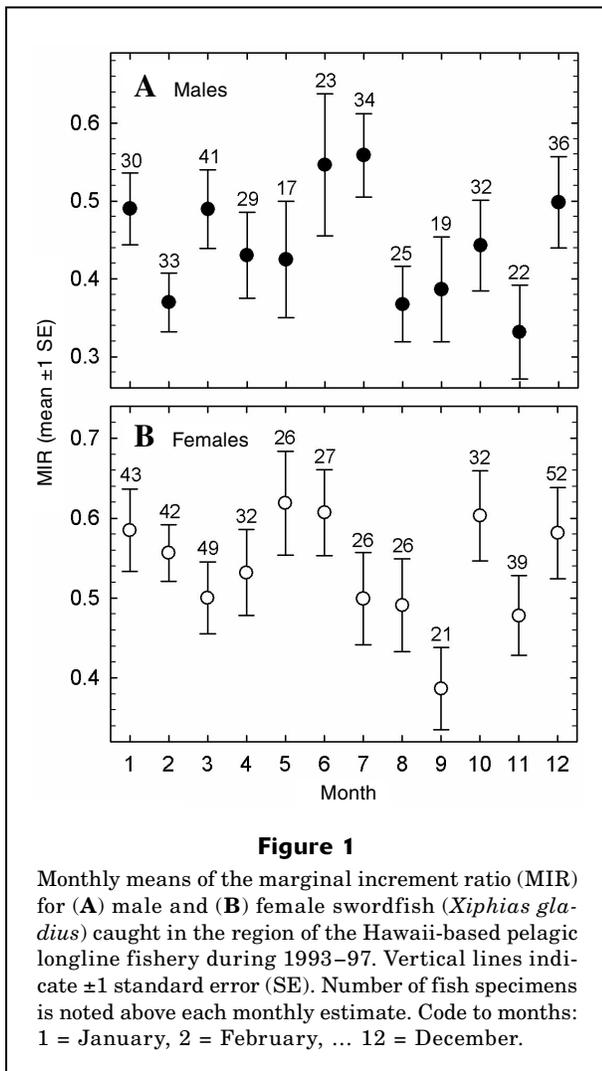


Figure 1

Monthly means of the marginal increment ratio (MIR) for (A) male and (B) female swordfish (*Xiphias gladius*) caught in the region of the Hawaii-based pelagic longline fishery during 1993–97. Vertical lines indicate ± 1 standard error (SE). Number of fish specimens is noted above each monthly estimate. Code to months: 1 = January, 2 = February, ... 12 = December.

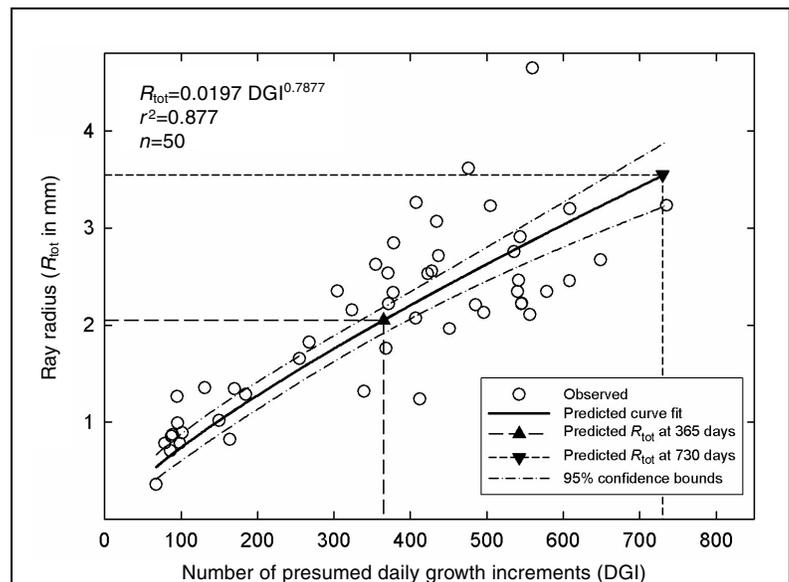
Table 2

Summary of eye-to-fork length (EFL, cm) statistics and estimated mean back-calculated lengths-at-age for swordfish (*Xiphias gladius*) of each sex and age-group, caught in the region of the Hawaii-based pelagic longline fishery during 1993–97. SD=standard deviation.

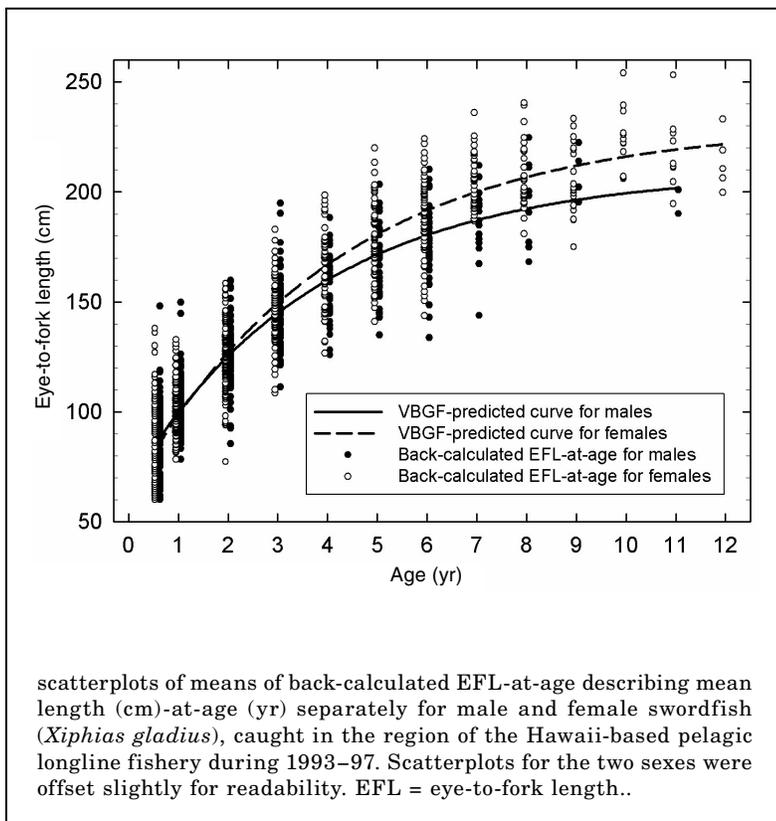
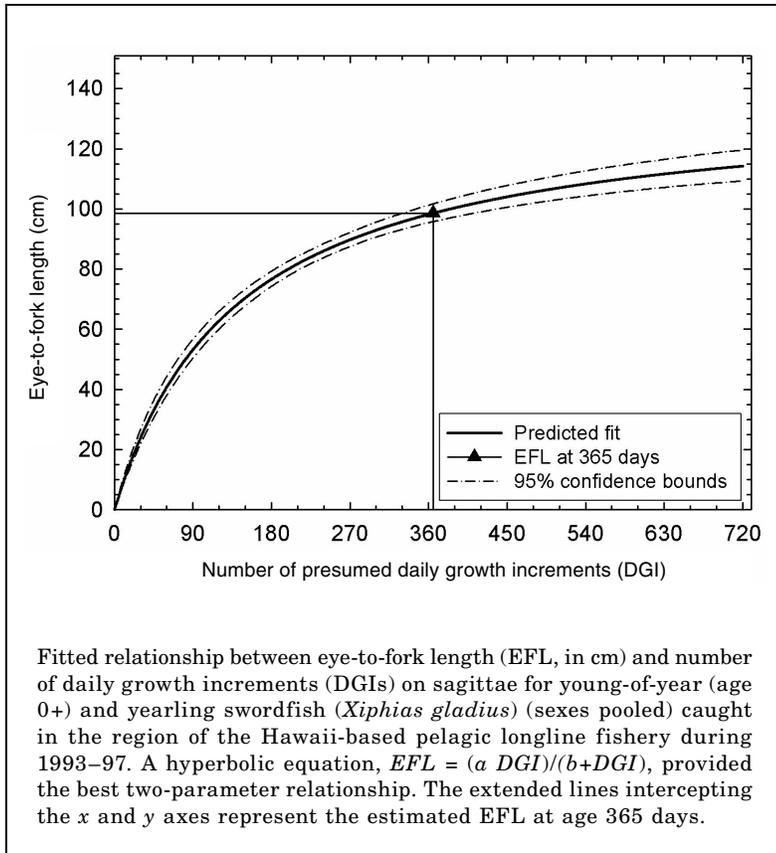
Age group	Males			Females		
	Sample size	Back-calculated EFL	Mean \pm SD EFL	Sample size	Back-calculated EFL	Mean \pm SD EFL
0	136		82.1 \pm 18.4	137		82.3 \pm 18.8
1	145	102.0	114.3 \pm 13.2	114	100.5	115.1 \pm 14.2
2	97	127.4	137.0 \pm 13.5	109	126.3	138.3 \pm 15.1
3	69	147.9	155.3 \pm 16.0	64	147.7	155.4 \pm 15.5
4	41	159.9	164.1 \pm 14.2	58	167.1	171.4 \pm 18.2
5	29	166.3	172.8 \pm 18.0	59	179.6	185.3 \pm 18.0
6	34	174.7	181.0 \pm 17.6	63	189.7	195.0 \pm 17.8
7	15	188.4	189.7 \pm 17.2	36	204.7	209.9 \pm 12.4
8	10	196.7	197.3 \pm 19.7	29	208.5	212.3 \pm 15.4
9	4	202.2	212.5 \pm 12.9	20	208.0	210.3 \pm 16.6
10				12	223.4	228.0 \pm 15.6
11	2	197.5	198.5 \pm 6.4	9	219.6	222.8 \pm 17.6
12				5	216.0	218.2 \pm 14.5

Back-calculated lengths-at-age were used to evaluate length versus age by using several versions of the von Bertalanffy growth model, for a total 1292 fish (712 females, 580 males) \geq 60 cm EFL. Less than 4% of all fin ray preparations were deemed unreadable and not used. Age-group-0 fish (0.58 yr; 82.3 cm [females], 82.1 cm [males]) were included in the model fits. Male and female swordfish clearly grow in length at different rates after age 1 (Table 4; likelihood-ratio test; $P < 0.001$; Table 5A). Furthermore, for central North Pacific swordfish spanning the length range of most fish in the commercial catch (60-cm EFL as an average minimum), the standard three-parameter VBGF fit the length-at-age data more efficiently than Richards' generalized VBGF (likelihood-ratio test; males: $P > 0.2$, females: $P = 0.5$; Table 5B). Hence, the standard VBGF is the more parsimonious growth model and should be applied to the sexes separately for central North Pacific swordfish of exploitable sizes (Table 4; Fig 4).

Three fish, whose ship-side, visually estimated weights were equivalent to lengths of 88, 98, and 93 cm EFL when initially tagged and released, were recaptured after 364, 610, and 1490 days at liberty and had grown 38, 58, and 90 cm, respectively, based on round weights at market (Uchiyama et al., 1998). The sex of none of these fish was determined when they were tagged



Scatterplot and fitted relationship between the total cross-section radius (R_{tot} , in mm) of the second ray of the first anal fin and the number of daily growth increments (DGI; estimated age in presumed days based on microincrement counts) on sagittae for the same young-of-year and yearling swordfish (*Xiphias gladius*) (sexes pooled) caught in the region of the Hawaii-based pelagic longline fishery during 1993–97. The power equation, $R_{tot} = a DGI^b$, was used to model the fitted relationship. The extended lines intercepting the x and y axes represent the estimated radii at ages 365 and 730 days. Confidence in the R_{tot} at age 730 days (3.5–3.6 mm) is low because of the poor readability of DGIs at and beyond this age, for fish of either or both sexes.



or recaptured. If estimated length increments are related to a fit of the standard VBGF (sexes pooled) for central North Pacific swordfish, the growth trajectories of these fish agreed reasonably well with those expected for fish of their sizes at liberty for the observed durations (Fig. 5).

Discussion

Verification and validation of age

Our comparisons of ages based on annuli in fin ray sections and DGIs in otoliths, coupled with those of ray radii and otolith ages, represent a novel approach to verifying the age and growth of swordfish and other species for which validation is difficult. The good agreement we observed between our estimates of size at age 1 yr based on fin rays provides a strong partial verification of our aging protocols for young swordfish. Our detailed cross-validation of fin ray annuli against otolith DGIs has conclusively identified the location of the first annulus on swordfish fin rays for the first time. Marginal increment analysis further corroborates that a single annulus forms once each year in anal-fin rays and is complete for swordfish through age 7 caught in the central North Pacific by the end of the spawning period in late summer (DeMartini et al., 2000), when somatic condition is lowest (Uchiyama et al., 1999). Others have similarly observed that the time of annulus formation occurs at the end of the growing season for swordfish in the western North Pacific (Sun et al., 2002) and eastern South Pacific (Cerna¹), although other drains on physiological condition, such as migration, may be involved (Sun et al., 2002). We also present final proof that basal cross sections of fin rays underestimate ages as a result of partial or complete resorption of the first annulus, as first proposed by Berkeley and Houde (1983) and subsequently observed by Tserpes and Tsimenides (1995) and others. Our comparison of age readings derived from basal, *d/2*, and suture terminus cuts of anal-fin rays demonstrates the equivalence of the latter two types of ray cross sections.

¹ Cerna, F. J. 2006. Unpubl. data. Sección Edad y Crecimiento, División de Investigación Pesquera, Instituto de Fomento Pesquero, Blanco 839, Valparaiso 5a Region, Chile.

Table 3

Mean R_n (radius from focus to distal edge of each annulus) for each age-group of male and female swordfish (*Xiphias gladius*) caught in the region of the Hawaii-based pelagic longline fishery during 1993–97. Roman numerals indicate the number of presumed annuli. SD = standard deviation. “Increment” refers to the increase in mean R_n from the preceding annulus.

Males Age-group (yr)	Sample size	Mean R_n (mm) from focus to distal edge of each annulus											
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	
0	136												
1	145	2.22											
2	97	2.23	3.34										
3	68	2.20	3.38	4.30									
4	41	2.17	3.36	4.32	5.04								
5	29	2.19	3.33	4.35	5.11	5.76							
6	33	2.09	3.27	4.25	5.09	5.87	6.43						
7	15	2.39	3.41	4.27	4.98	5.62	6.15	6.61					
8	10	2.08	3.23	4.19	4.87	5.53	6.09	6.57	6.96				
9	4	2.28	3.24	4.23	5.24	5.85	6.50	7.15	7.76	8.22			
10	—												
11	2	2.02	3.15	3.86	4.96	5.54	6.17	6.59	6.91	7.28	—		8.03
Mean		2.19	3.30	4.22	5.04	5.69	6.26	6.73	7.21	7.75			8.03
SD		0.11	0.09	0.15	0.12	0.15	0.18	0.28	0.48	0.66			—
Increment			1.11	0.92	0.82	0.65	0.57	0.47	0.48	0.54			0.28

Females Age-group (yr)	Sample size	Mean R_n (mm) from focus to distal edge of each annulus											
		I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII
0	137												
1	114	2.22											
2	108	2.26	3.37										
3	63	2.15	3.36	4.28									
4	58	2.15	3.25	4.22	4.99								
5	58	2.27	3.42	4.40	5.28	5.95							
6	63	2.17	3.28	4.29	5.25	6.04	6.65						
7	36	2.24	3.42	4.47	5.42	6.16	6.79	7.25					
8	29	2.23	3.31	4.24	5.14	5.88	6.56	7.19	7.62				
9	20	2.15	3.27	4.20	5.06	5.75	6.39	6.98	7.48	7.89			
10	12	2.13	3.23	4.19	5.08	5.94	6.60	7.21	7.75	8.24	8.67		
11	9	2.18	3.11	4.02	4.99	5.77	6.52	7.19	7.71	8.14	8.56	8.90	
12	5	2.28	3.31	4.33	5.14	5.71	6.40	6.97	7.45	7.90	8.34	8.70	9.08
Mean		2.20	3.30	4.27	5.15	5.90	6.56	7.13	7.60	8.04	8.52	8.80	9.08
SD		0.05	0.09	0.12	0.14	0.16	0.14	0.12	0.13	0.17	0.17	0.14	
Increment			1.10	0.97	0.88	0.75	0.66	0.57	0.47	0.44	0.48	0.28	0.28

Selection of growth model

Unlike swordfish caught in waters near Taiwan (Sun et al., 2002), swordfish of exploitable size in the central North Pacific near Hawaii grow in length at rates best described by the standard, rather than generalized, VBGF. We suggest that this model primarily reflects the different size structure of catches from the two regions. By truncating the application of our growth model at the approximate minimum size of fish caught by the Hawaii-based longline fishery (60-cm EFL), we eliminate the markedly allometric growth effects that half-year-old and younger fish have on the ascending limb of the VBGF curve. The disproportionately low body mass of

young juveniles reflects the fact that swordfish, perhaps like most pelagic fishes that are reliant on swimming speed as their primary antipredator adaptation (and unlike typical nonpelagic fish with less pronounced allometric growth), must experience intense selection for growth in length (swimming speed) at the expense of growth in mass during the juvenile stage. A related issue is the fact that swordfish >180–200 cm EFL are more abundant in the Hawaiian than in Taiwanese fisheries, and these larger fish provide an extended scope for resolving the asymptote of VBGF models, especially the standard VBGF which lacks a fourth parameter (shape function) to help resolve curvature of the ascending limb. Not surprisingly, growth of swordfish caught

Table 4

Parameter estimates (\pm standard error, SE) for the standard von Bertalanffy and the generalized von Bertalanffy growth formulas (VBGFs) fitting mean back-calculated eye-to-fork length (EFL)-at-age against age for male and female swordfish (*Xiphias gladius*) ≥ 60 cm EFL caught in the region of the Hawaii-based longline fishery during 1993–97. L_{∞} = asymptotic length; k and K = growth coefficients; t_0 = hypothetical age at length zero; m = fitted fourth parameter; n = number of age-classes. r^2 = coefficient of determination; n = sample size.

Parameter	Standard VBGF		Generalized VBGF	
	Male	Female	Male	Female
L_{∞}	208.9 \pm 5.60	230.5 \pm 3.94	221.0 \pm 20.1	227.2 \pm 6.18
k	0.271 \pm 0.034	0.246 \pm 0.019		
K			0.070 \pm 0.080	0.524 \pm 0.871
t_0	-1.37 \pm 0.259	-1.24 \pm 0.167	-0.15 \pm 0.576	-2.41 \pm 2.968
m			-1.27 \pm 1.122	0.448 \pm 0.771
r^2	0.989	0.995	0.991	0.995
n	11	12	11	12
P	<0.001	<0.001	<0.001	<0.001

Table 5

Summary statistics for likelihood ratio (LR) tests evaluating (A) potential differences between the estimated von Bertalanffy growth (VBGF) parameters for male and female swordfish (*Xiphias gladius*), and (B) the standard versus generalized VBGF models of length-on-age for males and females caught in the region of the Hawaii-based pelagic longline fishery during 1993–97. H_0 = null hypothesis.

	Sexes pooled		By sex (male+female)	
	Standard	Generalized	Standard	Generalized
A Male versus female				
Log-likelihood		-64.7		-79.1
X^2 (prob $> \chi^2$)		28.8 (<0.001)		
Conclusion		Reject H_0 : male = female		
	Male		Female	
	Standard	Generalized	Standard	Generalized
B Standard versus generalized VBGF				
Log-likelihood	-30.7	-29.9	-34.0	-33.8
X^2 (prob $> \chi^2$)	1.62 ($P > 0.2$)	0.46 ($P = 0.5$)		
Conclusion	Accept H_0 : standard = generalized		Accept H_0 : standard = generalized	

by the Chilean longline fishery (Cerna¹), like those caught near Hawaii, is better described by the standard VBGF, and large swordfish are also abundant in the relatively undeveloped Chilean fishery. Chapman's five-parameter version of the generalized VBGF would be the most appropriate for describing size-at-age of swordfish only if there was a compelling reason to fit the growth curve through zero length at zero age (see Arocha et al., 2003).

Our growth-at-liberty data for tagged-recaptured swordfish in the central North Pacific, albeit limited to only three fish, are consistent with modeled growth of small- to medium-size adult fish. Restrepo (1990) and Brown (1995) provide the only other data of this type for swordfish, limited to fish caught in the Atlantic

Ocean and Gulf of Mexico. The usefulness of such data is limited because of inaccuracies in estimates of body size at time of first capture (Restrepo, 1990)—as it was for our tagged swordfish—and uncertain units of size measurement (Brown, 1995), but some general growth patterns are nonetheless evident. For nearly 100 swordfish with a median length of about 100 cm at initial capture and of 135 cm when recaptured after a median period at liberty of 1.5 years, the growth rate was about 24 cm per yr (Brown, 1995). Given that body size when a fish is tagged is usually overestimated (Restrepo, 1990), and this body size yields an underestimate of incremental growth at liberty and given also the likely faster growth of swordfish in the Pacific—especially the central North Pacific—see below, the average growth in-

crement (35 cm per yr) that we observed for the three tagged-recaptured fish, yearlings in size when first caught and at liberty for 1, 2, and 4 years, is reasonable, as well as consistent, with our modeled growth trajectories for fish of this size range. We nonetheless caution, however, that these few consistencies by themselves do not verify our growth curves.

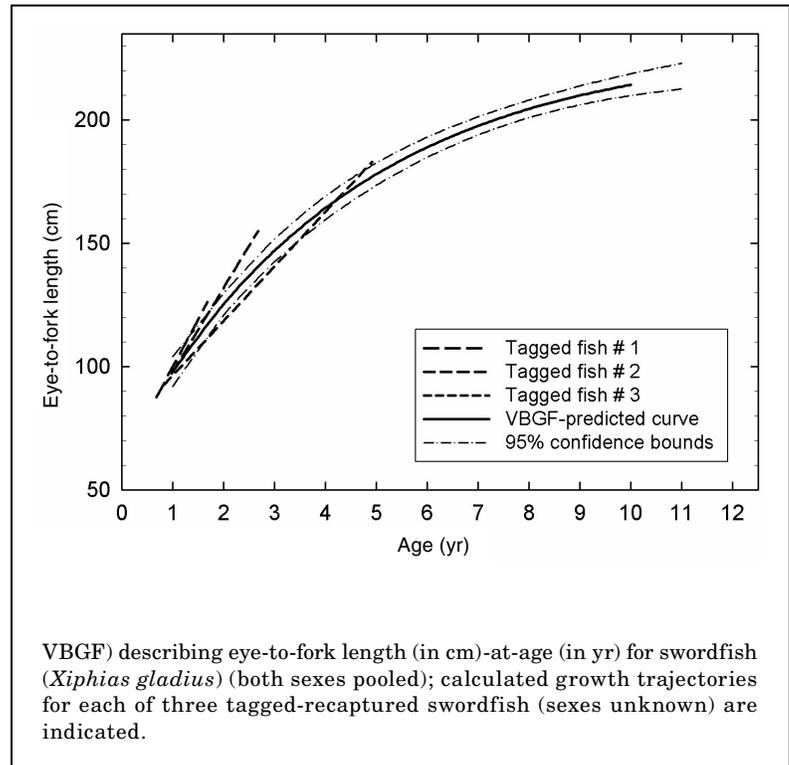
Sexually dimorphic growth

By now there can be no doubt that female swordfish grow faster and attain larger maximum body sizes than do males in the Pacific (Castro-Longoria, 1995; Sun et al., 2002; Cerna¹; this study), as many others (e.g., Berkeley and Houde, 1983) have observed for swordfish in the Atlantic. That females on average live longer than males is less certain, and this uncertainty will likely persist because of the rarity of the largest, oldest fish captured by fisheries—especially in developed fisheries—and associated difficulties in validating estimates of their ages. Even though sexually dimorphic growth does not become prominent in either body length or fin rays until after age 1, it is obvious that the sexes should be evaluated separately in stock assessments (Wang et al., 2005) for retained swordfish (generally greater than 1 yr old in most fisheries) whenever landings data allow. The sexual differences in body size and growth that we observed reinforce the argument that sex-specific, age-based stock assessments are needed for swordfish.

The greater probability of error in estimating the ages of larger swordfish affects females disproportionately as the larger-bodied fish. Sex-specific stock assessments need to explicitly evaluate the greater uncertainty of age estimates for the largest, mostly female, fish as well as the more generally recognized influences of gear bias on the capture efficiency (hence sex ratio) for male and female swordfish of different sizes.

Unresolved issues and future research needs

In prior studies of swordfish age and growth there has been the conspicuous need to validate the periodicity of annulus formation for all age groups present in a fishery, including the oldest age groups, which are typically relegated to a catch-all plus group that complicates stock assessment computations (Restrepo and Powers, 1991). Validation of the age and growth of these largest, oldest fish likewise has been a problem in our study, and our estimates of growth-at-liberty for tag-recaptured fish only provide insights into growth (not absolute age) of juveniles and young adults. There is still great need to verify the accuracy of age estimates for swordfish in older age-groups. Radiometric aging (Watters et al.,



2006), one alternative method for aging the hard parts of large, old fish, is inappropriate for swordfish because the oldest living tissue is reabsorbed within fin rays and because their tiny otoliths provide insufficient material for analysis of individual fish. Resolution of the problem would almost certainly require a dedicated, large-scale, and expensive conventional tagging effort targeting large and old fish, preferably one in which a rigorous protocol is implemented for accurately estimating size at initial capture and labeling body size at time of release with a fluorescent biomarker. Such a study is unlikely to be implemented unless greater reductions in stock sizes, increases in value, or (more likely) both in concert, justify the great cost of such an enterprise. Of course, such a study could provide data on fish movements whose importance might dwarf that of age and growth validation.

Geographic variation in growth rates is evident for swordfish in regional Pacific fisheries. Size-at-age is appreciably greater for swordfish caught in the region of the Hawaii-based fishery (versus the Taiwanese fishery) and the regional difference includes juvenile and small adult, as well as larger adult fish. For example, the mean length at age 1 of swordfish in the Taiwanese fishery is about 96 cm lower-jaw-to-fork length, which is equivalent to only 83 cm EFL (Sun et al., 2002), whereas the mean length at age 1 in the Hawaii-based fishery is 99 cm EFL. The results of our study indicate that swordfish caught in the central North Pacific grow in length at a rate faster than swordfish caught by several other Pacific regional fisheries (Fig. 6), and this

finding was confirmed by readers from other laboratories during the inter-laboratory exercise. Faster growth in the central North Pacific (versus the western North Pacific) may reflect the high planktonic productivity of swordfish feeding grounds in the Subtropical Convergence Zone (Seki et al., 2002), perhaps similar to that in the productive upwelling region off Chile in the eastern South Pacific. Consistent with this observation, data on body condition (weight-at-length) indicate that central North Pacific swordfish are heavier at a given length than swordfish from the western North Pacific (Uchiyama et al., 1999; Sun et al., 2002). Regional differences in growth rates are also apparent for swordfish

throughout the Atlantic and Mediterranean (Tserpes and Tsimenides, 1995; Ehrhardt et al., 1996; Alici and Oray, 2001).

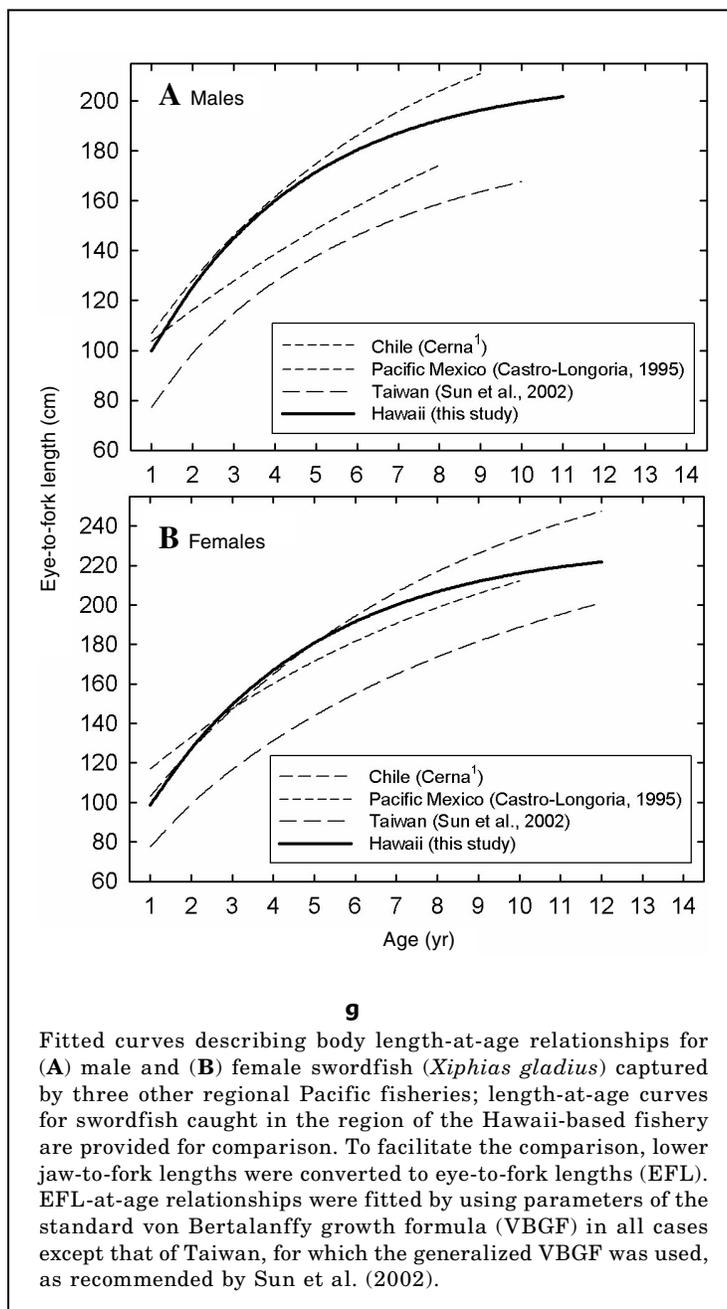
Stock structure is still incompletely understood for Pacific swordfish and regional variations in growth rates complicate rather than resolve the issue. Present understanding of the population genetics of swordfish indicates that separate stocks exist in the North and South Pacific and that there likely is some stock structuring between east and west in the North Pacific (Reeb et al., 2000). Detailed comparisons among the nuclear (microsatellite) DNAs and mtDNAs of planktonic spawning products (eggs and larvae) and fish of exploitable sizes, coupled with analyses of phenotypic traits like growth and environmental markers, such as trace element signatures in otoliths (Humphreys et al., 2005), are needed for swordfish collected from all regional fisheries in order to fully resolve the stock issue for swordfish in the Pacific.

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